

## Phylogenetic, habitat, and behavioural aspects of possum behaviour in European lepidoptera

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**Abstract:** We describe the behaviour of playing possum, or thanatosis, in mate rejection by non-receptive female butterflies of the Satyrinae of the Palearctic. In this behaviour females feign death with closed wings and release themselves from the substrate on which they are settled. This behaviour only occurs with extreme male persistence and is the final part of a mate-rejection behavioural sequence. We suggest that this behaviour may be relatively rare, possibly restricted to the tribes Elymiini and Maniolini. There are potential associations with female mating frequency, male mate-locating mechanisms and the physical structure of habitats where attempted mating occurs. We suggest that the behaviour occurs in species where females occasionally mate more than once, where the predominant male mating strategy is a perching sit-and-wait tactic and the species occupy woodland structures. In such circumstances males have relatively few opportunities to mate, male-female encounter rates may be relatively infrequent and the physical structure of the habitat allows females that adopt possum mate-rejection to escape from males by dropping into vegetation. We encourage further observations on this behaviour to allow a thorough analysis of its frequency amongst species in order to allow a phylogenetic analysis.

**Key words:** predation, mate location, mate rejection, *Pararge*, *Lasiommata*, *Kirinia*, *Esperarge*, *Maniola*.

Playing possum (thanatosis: feigning death) in butterflies has been described for two very different circumstances. It was first described as a predator escape mechanism in *Gonepteryx rhamni* L. Pieridae (Dennis 1984) and *Inachis io* L. Nymphalidae (Dennis 1998). More recently, it has also been shown to have a role in mate refusal by females of *Pararge* and *Lasiommata* species (Satyrinae) (Shreeve 1985, Dennis 2003) and has been described for *Esperarge climene* (Satyrinae) (Wakeham-Dawson et al. 1999). As far as we are aware it has not been described in mate rejection for any other butterfly taxon apart from Satyrinae (nomenclature as in Karsholt & Razowski 1996). Here, we summarise the behavioural, morphological, habitat and phylogenetic attributes for these behaviours as

currently known; in doing so we focus attention on possum behaviour in mate rejection, the objective being to encourage further observations (Table 1).

In the Lepidoptera possum behaviour is a widespread secondary defence mechanism (Scoble 1992) and in the butterflies it has been recorded in species of Nymphalinae and Pieridae. On being caught by the wings, these species undergo thanatosis and effectively play dead. When released they will lie on their side inert for some time before taking flight (Dennis 1984, 1998). Species which adopt this behaviour tend to be long-lived and have relatively robust wings. As manipulation by birds can lead to wing damage, evidenced in tears and scored beak marks across wings of butterflies caught by birds (Collenette 1935, Bowers & Wiernasz 1979, Bengston 1981, Dennis et al. 1984), this would give butterflies with tougher wings an advantage over those with weaker structures. Butterflies described

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displaying possum behaviour in relation to predation typically hibernate as adults and have under-surfaces and wing shapes that characteristically mimic dead leaves. They spend much of the later summer feeding avidly on nectar and in such situations are particularly vulnerable to predation. *G. rhamni* are often so engrossed in feeding that they can be picked off the flower heads with ease (Dennis 1984). Experiments on possum behaviour indicate that the behaviour may be triggered more easily in autumn brood adults intent on accumulating resources for hibernation than in early summer broods actively engaged in mating. Although described thus far for *G. rhamni* and *I. io*, it is expected that this behaviour will extend to closely related species with similar life histories, morphology and behaviour (e.g., *Aglais urticae*).

Possum behaviour in mate rejection is the final stage of a behavioural sequence, with common elements to more normally widespread mate rejection behaviour. First, when harassed by a male attempting to copulate, a settled female may simply raise its abdomen to prevent copulation (e.g., *Pieris napi* L. Pieridae; *Plebejus argus*, L. Lycaenidae; Wilcockson 2002, Dennis, pers. observation). This may or may not involve wing fluttering as well. This behaviour, which may involve exposure of the genitalia with possible chemical signalling, is common to many butterfly taxa (Obara 1982, Obara 1984), but not all. In butterflies that adopt abdominal raising, there may be a second stage of mate-rejection in which a non-receptive female may attempt to prevent mating by completely closing its wings if the initial abdominal-raising proves unsuccessful. In butterflies that do not adopt abdominal raising, wing closing is usually the first stage to prevent mating by a persistent male. The genitalia of a closed wing female are then completely inaccessible to the courting male. Where possum behaviour differs from ordinary wing closing is in the subsequent stages. In possum-playing females the harassed female may lean over onto the substrate, effectively playing dead. Should the male persist then the female may then release its tarsal claws from the substrate on which it is settled and drop to lower vegetation or even the ground. In most instances when this occurs in *Pararge aegeria* L., and in the described behaviour of *Esperage climene* Esper, the male will lose the female and fly off (Shreeve 1985, Wakeham-Dawson et al. 1999). In other instances the male will pursue the female to the lower substrate or ground and persist in trying to enforce copulation before eventually giving up and flying off. This persistence may be long (max 65 sec. in *Pararge aegeria*, Shreeve 1985). In no instance has successful copulation of the apparently 'dead' female been recorded, either before or after

falling from a substrate. When a refusing female plays possum it will remain quiescent after the male leaves before resuming its activities (flight or basking). The two stages of orientation and dropping make possum behaviour unique. It appears to be part of females' mate-rejection repertoires when the total duration of male harassment is very long (Dennis 2003).

Recorded instances (Table 1) of females playing possum behaviour in response to attempted copulation by males is possibly restricted to the tribe Elymniini and one member of the tribe Maniolini, *Maniola jurtina* L. (Satyrinae, Maniolini). In the case of *M. jurtina*, this behaviour has been recorded in 4 instances out of 27 attempted courtships in dry Mediterranean scrub/woodland in Provence, France observed between 27 July and 11 August 1988 by one of us (TGS). As far as we are aware possum behaviour linked to mate-rejection has not been recorded in any higher taxa. Instances of similar, but not identical, behaviour are described in *Carterocephalus palaemon*, Hesperiiidae (Ravenscroft 1994: 1185) and females of other species will reject males by remaining quiescent during attempted courtships (e.g., *Leptidea sinapis* L. Dismorphiinae; Wiklund 1977). In the case of *C. palaemon* unreceptive females drop to the ground with closed wings when pursued by a flying male and the behaviour of *L. sinapis* is different from true possum behaviour in that unreceptive flying females detected by flying males sail to the vegetation and rest quiescent with closed wings. Restricting the analysis to the Satyrinae reveals that there are potential associations with female mating frequency, male mate-locating mechanisms and the physical structure of habitats where attempted mating occurs. Possum behaviour has not been recorded in those taxa where male access to already mated females is physically obstructed by a sphragis (mating plug) (e.g., *Hipparchia*, *Heteronympha*; Orr 2002). On the other hand, it has been recorded in those members of the Elymniini (*Pararge aegeria*, *P. xiphia* Fabricius, *P. xiphoides* Staudinger) and in *Maniola jurtina*, (Shreeve 1985, Dennis 2003, J. Tennent, personal communication) where females may occasionally mate more than once (*P. aegeria* 4–10% Wickman & Wiklund 1983, Shreeve 1985; *P. xiphia* 5% and *P. xiphoides* 8%, Shreeve unpublished; *M. jurtina* 4%, Maier, 1998) The mating frequency of *Esperage climene*, in which possum behaviour occurs, is not known. With one exception, female possum behaviour in mate-rejection has only been recorded in species in which the primary mechanism of mate-locating by males is perching and where perching occurs in predictable woodland structures, with males primarily settled on vegetation above the ground. Partial possum behaviour (in which females do not release

Table 1. The occurrence of possum behaviour in relation to habitat structural associations, mate locating methods, female mating frequencies and congruence of hostplants with mating areas in Palearctic butterfly taxa

Super-family	Family	Subfamily	Tribe/Species	Possum behaviour	Habitat structure	Primary male mate-locating mechanism	Female mating frequency	Egg-laying and mating location congruence	Hostplant location selectivity by laying females
Hesperioidea	Hesperiidae			-	Open short-medium length grassland and wasteland	Perching & patrolling	?	Variable	High
Papilionoidea	Papilionidae			-	Open grassland, scrub and scree	Perching or patrolling	Single	Variable	High
	Pieridae	Dismorphinae		-	Open grassland	Patrolling	Single	High	High
		Pierinae		-	Riparian, wet grassland, pioneer	Patrolling	Multiple	High	High
		Coliadinae	<i>Colias</i> spp.	-	Open grassland	Patrolling	Multiple?	High	High
			<i>Gonepteryx</i> spp.	AP	Woodland and scrub	Patrolling	Single	Low	High
	Lycaenidae			-	All	Perching, lek or patrolling	?	Variable	High
		Libytheinae		?	Open woodland	?	?	?	High
		Heliconiinae		?					?
		Nymphalinae		AP	Open grassland, fen, scrub, woodland	Perching & patrolling	?	Variable	High
		Limentinae		-	Woodland	Perching	Single?	Low	High
		Charaxinae		?	Woodland edge	Patrolling	?	Low	High
		Apaturninae		-	Woodland	Perching	?	Low	High
		Satyrinae							
			Elmmini						
			<i>Kirina roxelana</i>	?	Woodland	Perching		High	High
			<i>Esperage climene</i>	+	Woodland	Perching		High	High
			<i>Pararge aegeria</i>	+	Woodland	Perching		High	High
			<i>Pxiphia</i>	+	Woodland	Perching	Multiple	High	High
			<i>P.xiphoides</i>	+	Woodland	Perching	Multiple	High	High
			<i>Lasiommata megera</i>	-	Open grassland, pioneer, scrub	Perching	Multiple	High	High
			<i>L.petroplitana</i>	-	Open grassland	Perching	?	High	High
			<i>L.paramegaura</i>	-	Open grassland	Perching	?	High	High
			<i>L.maera</i>	-	Open grassland	Perching	?	High	High

Table 1 cont.

Super-family	Family	Subfamily	Tribe/Species	Possum behaviour	Habitat structure	Primary male mate-locating mechanism	Female mating frequency	Egg-laying and mating location congruence	Hostplant location selectivity by laying females
			<i>L. deidama</i>	?	Open grassland	Perching	?	High	High
			<i>Lopinga achine</i>	+	Woodland	Perching	?	High	High
			Ypthimini						?
			Coenonymphini	-	Open grassland/ pioneer structures/ scrub/bogs	Perching	?	Variable	High
			Maniolini						
			<i>Pyronia</i> spp.	-	Grassland/scrub	Patrolling	?	Low	Low
			<i>Aphantopus hyperantus</i>	-	Open grassland	Patrolling	?	Low	Low
			<i>Maniola</i> spp.	+ in <i>M. jurtina</i>	Open grassland	Patrolling	Multiple	High	Low
			<i>Hyponephele</i> spp.	?	Scrub and scrub	Patrolling?	?	?	?
			Erebini	-	Grassland and open structures, bogs	Patrolling	?	Variable	Variable
			Satyrini						
			<i>Satyrus</i> spp.	?	Open grassland	Patrolling	?	High	Low
			<i>Minois dryas</i>	?	Open grassland	Patrolling	?	Low	Low
			<i>Hipparchia</i> spp.	-	Pioneer structures/ open grassland	Perching	Single	Low	Low
			<i>Arctusena arethusea</i>	-	Pioneer structures/ open woodland	Perching	Single	Low	High
			<i>Brintesia</i> spp.	-	Scrub/woodland	Perching	Single	Low	High
			<i>Chazara</i> spp.	?	Pioneer structures	Perching	Single	Low	High
			<i>Pseudochazara</i> spp.	?	Pioneer structures	Perching	Single	Low	High
			<i>Oeneis</i> spp.	?	Pioneer structures	Perching	?	Low	High
			Danaeinae	-	All except woodland	Patrolling	Multiple	Low	High

Nomenclature follows Karsholt & Razowski (1996)

+ recorded as occurring, - recorded as not occurring, ? no data, AP predator escape mechanism

Multiple female mating frequency = known instances of females mating more than once

from the substrates they are on) occurs within the *Lasioommata* genus, but in all instances occurrences have taken place on bare ground substrates (T.G. Shreeve, personal observation). Recorded instances of possum behaviour by females of *Maniola jurtina* have been in woodland structures in southern Europe where summer aestivation occurs. With the exception of *Maniola jurtina*, females that adopt possum behaviour are also highly selective of the locations in which they lay eggs, even if plant species on which larvae feed are themselves widespread.

Whilst information on the details of mate rejection by females of the majority of species is extremely scant, the provisional analysis that we supply here is itself revealing of a possible phylogenetic component with links to the overall behaviours of both sexes and the physical structure of the habitats in which species occur. The occurrence of female possum behaviour as a mate rejection behaviour can be explained by a common set of characteristics; females potentially mating more than once, occupation of specific woodland structures, the occurrence of perching within the mate locating repertoire and selectivity by females for specific egg-laying locations. A common element of female possum behaviour is that it only occurs after other mate-rejection postures, such as abdominal raising, wing fluttering and wing closing, have failed to deter the male. It is also potentially time consuming for both the male and even more so for the female, which will tend to remain quiescent after the courting male has left.

If females easily and unequivocally communicate their non-receptivity then it is pointless for any male to spend time attempting to court a non-receptive female. In such circumstances it is unlikely that female possum behaviour will be employed or even develop. Thus the behaviour is absent where there is the clear signal of a sphragis in single mating females (e.g., *Hipparchia*; Satyrinae). It is also absent where there is multiple mating, but unreceptive females are plugged with a sphragis and males have limited resources to make plugs (e.g. *Heteronympha* species) or where effective chemical signalling associated with abdominal raising occurs in potentially multiple mating females (e.g. *Pieris* spp.; Pieridae, Obara & Hidaka 1964). It is also apparently absent in species in which receptive females have specific behaviours to advertise their receptiveness to males such as the jumping flights of virgin *Aphantopus hyperantus* L. (Maniolini) (Wiklund 1982). Efficient communication of receptiveness is advantageous to females since they will not spend time harassed by males. When males are given an unambiguous early cue of non-receptivity then they are unlikely to harass, so more complex rejection

behaviours may not be developed.

In species in which female possum behaviour occurs the primary male mate locating mechanism is perching. Perching males sit and wait for females and their persistence with individual females may be high to try and enforce copulation with relatively scarce females. If mated females fly into areas where perching males detect them they do so because they are searching for other resources (e.g. egg-laying sites, nectar sources). In the case of *Pararge* species, females are highly selective of egg-laying sites (e.g. Shreeve 1985, 1986, Shreeve & Smith 1992) and possum behaviour may be the only sure mechanism of deterring a courting male if the female is in a suitable egg-laying location. Time spent playing possum may be less than time spent searching for alternative resources elsewhere. In the case of *Pararge aegeria*, the maximum recorded time playing possum (65 seconds) is within the range of times spent on searching flight between egg-laying locations (Shreeve 1985).

Female possum behaviour may be absent in strictly patrolling species. We suggest that it has not developed in this circumstance because in such species females are readily apparent to males by colouration (Dennis & Shreeve 1988) or are abundant. Thus it may be unproductive for males to persist with an unreceptive female since others will be readily detected or encountered. Similar arguments apply to lekking species (e.g. some Theclinae); the majority of females entering a lek will be receptive.

Although we have limited data, it is possible that female possum behaviour may be restricted to species that use a specific set of woodland structures, though not universally so. For example, it has not been recorded for species that locate mates primarily within the woodland canopy (e.g. *Argynnis* species, Nymphalidae; *Neozephyrus* species, Lycaenidae) or on the ground layer of woodland (e.g. *Arethusena* species, Nymphalidae).. One key characteristic of those species that use this form of possum behaviour is the resemblance of the wing underside to dry leaves, which are predictable components of the ground layer. As examples, *Argynnis* and *Neozephyrus* species may be highly conspicuous to conspecifics and predators when on the ground layer and adoption of possum behaviour may increase predation risk. The absence of possum behaviour from multiple mating species of grassland and more open structures such as rock slopes may also be related to wing and substrate colouration, with the latter tending to be more variable than in woodland. In such circumstances any individual playing possum may render itself conspicuous and vulnerable to predation. We suggest that contrast of underside wing colouration with background is itself a constraint on

the development of possum behaviour.

Whilst the information on this behaviour is rather limited there are indications that it may also have a phylogenetic component. The adoption of possum behaviour in mate-rejection appears restricted to one or perhaps two tribes of the Satyrini. It may also be a derived trait associated with their adoption of woodland structures from ancestral open grassland structures (Dennis & Shreeve 1988). Evidence for the possible restriction of possum behaviour to the tribe Elymiini within the Satyrinae comes from its apparent absence from the behavioural repertoire of *Lethe diana*, which also occupies woodland structures (Ide 2002). Where possum behaviour occurs in other taxa (e.g. Nymphalinae and Pieridae), as indicated above, it is a primary response to predator attack and the species which adopt such a behaviour are long lived and have relatively thicker and more robust wings than the Satyrini (Table 1). We suggest that a more detailed examination of possum behaviour would reveal much about the interrelationship of behaviour with habitat structural predictability and costs and benefits of individual behavioural traits. In particular, information on the extent of its occurrence is required for a full analysis and a proper test of hypotheses to account for its occurrence. We would welcome observations.

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